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Tansley review

The hidden side of plant invasions: the role of genome size

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Summary

The ecological role of genome size in plant biology, biogeography, and morphology has garnered increasing attention as the methods and technology associated with measuring cytological characteristics have become more reliable and accessible. However, how plant genome size influences plant invasions and at what stage in the invasion this influence occurs have been little explored. Several large-scale analyses of published data have yielded valuable interspecific comparisons, but experimental studies that manipulate environmental factors are needed, particularly below the species level, to fully understand the role that genome size plays in plant invasion. In this review, we summarize the available knowledge, discuss the integration of genome size data into invasion research, and suggest how it can be applied to detect and manage invasive species. We also explore how global climate change could exert selective pressures on plant populations with varying genome sizes, thereby increasing the distribution range and invasiveness of some populations while decreasing others. Finally, we outline avenues for future research, including considerations of large-scale studies of intraspecific variation in genome size of invasive populations, testing the interaction of genome size with other factors in macroecological analyses of invasions, as well as the role this trait may play in plant–enemy interactions.

I. Introduction

The genome represents a distinct and legitimate level of biological organization within a cell, having its own unique evolutionary history and with genome size (GS) as one of its inherent properties. Although some DNA in eukaryotic cells is present in mitochondria and plastids, it is the nucleus that carries most of the hereditary material. One feature that has long puzzled researchers measuring

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nuclear GS is the tremendous variation encountered in many different groups of organisms (Gregory, 2005). Although the full biological significance of this variation remains unclear (see the *C*-value paradox/enigma; Gregory, 2001), data that have accumulated over the past decade increasingly show how the amount of nuclear DNA is involved in the scaling of living organisms and how it influences characteristics from the subcellular to organismal levels, irrespective of the coded information (the nucleotypic effect; Bennett, 1971). DNA therefore seems to play a dual role in heredity: genic – that is, storing the precise information about an organism's development and functioning; and nucleotypic – that is, setting thresholds within which the genes can operate and thus constraining an organism's functional traits independently of the information encoded in the DNA.

It has become increasingly clear that GS has considerable ecological significance, influencing where, when and how plants grow (e.g. reviewed in Greilhuber & Leitch, 2013). Nevertheless, the role of small vs large genomes in plant invasions is still poorly understood. For example, it may not be GS *per se* that contributes to invasiveness, but cell volume and cell growth rate that matter for adaptation of plants and other eukaryotic organisms to different niches (Cavalier-Smith, 2005). Genome size often tracks changes in cell size and growth rate that occur during evolution and this may arise through selection for the optimal karyoplasmic ratio, as suggested by Cavalier-Smith (2005). If this is the case, GS may not causally determine cellular characteristics but can serve as a useful marker for the net outcome of this coevolution because of its convenient quantification.

This review builds on and complements our previous work (te Beest *et al.*, 2012), which thoroughly explored the effects of genome duplication on invasion potential, and focuses on GS to elaborate on the role played by these cytological characteristics in plant invasions.

1. The state of the knowledge of plant genome size

Most questions investigating the impact of GS on plant traits require large amounts of data with broad taxonomic and geographic samplings. The major source of nuclear DNA amounts for photosynthetic eukaryotic organisms is the Plant DNA *C*-values database (http://data.kew.org/cvalues). The latest release (Bennett & Leitch, 2012) harbours nearly 12 500 records for algae, bryophytes, pteridophytes (comprising lycophytes and monilophytes (i.e. horsetails, whisk ferns, and eusporangiate and leptosporangiate ferns)), gymnosperms and angiosperms, 8509 of which represent 'prime' estimates (i.e. a preferred value for a given species if several estimates have been published). Currently, GS data are available for 7135 angiosperms (*c.* 2.0% coverage of their total diversity), 340 gymnosperms (*c.* 33%) and 121 pteridophytes (*c.* 0.9%) (note that these numbers are lower than the number of 'prime' estimates noted earlier because of the incidence of intraspecific ploidy diversity). As with any other crowd-sourced data, GS estimates listed in the Plant DNA *C*-values database are taken from the literature and have therefore been generated by multiple laboratories using a variety of methods (see Section I.2) and protocols, sometimes even before the methodological standards were set. The values should thus not be accepted uncritically or employed in all studies. While large-scale comparative analyses (e.g. invasive vs noninvasive species) based on database estimates are sufficiently robust, interpretation of small differences (e.g. intraspecific variation in *C*-values) is often unreliable; such investigations require sample processing in a single laboratory using best-practice approaches to ensure that any differences in GS are genuine and biologically significant rather than artefacts (Doležel *et al.*, 1998, 2007a).

The widespread occurrence of whole-genome duplications (polyploidy) in many plant groups, particularly angiosperms and pteridophytes, can give rise to potential problems regarding the use and meaning of the term genome size, because it has been used inconsistently in the literature. While some authors use GS to describe the total DNA content of the nucleus (i.e. in the complete chromosome complement) irrespective of the ploidy level of the organism, others use it to refer to the size of only one of the chromosome sets in the nucleus. To solve this problem, Greilhuber *et al.* (2005) suggested that specific adjectives be used and distinguished the holoploid GS and monoploid GS (Table 1).

Both holoploid and monoploid GSs vary greatly across vascular plants, but distinct patterns exist between the major evolutionary lineages in terms of the range and distribution of GS values (Fig. 1). Monilophytes typically possess genomes composed of many small chromosomes, possibly originating from multiple polyploidization events, and this variation manifests in comparatively large and variable genome sizes, with 1*C*-values ranging 94-fold. Genomes of gymnosperms are also relatively large but less dynamic in terms of both the frequency of polyploidy and the activity of transposable elements (Leitch & Leitch, 2012), resulting in limited variability in GS (1*C*-values range 16-fold). In contrast to gymnosperms, the evolution of angiosperm genomes is considered fast, driven by both genomic (e.g. higher frequency of polyploidy and interspecific hybridization, higher illegitimate and unequal homologous recombination, higher (retro)transposition) and ecological factors (e.g. shorter generation time, smaller population sizes, growth form diversity). Consequently, the diversity of genome sizes in angiosperms is unparalleled relative to any other lineage of vascular plants, with 1*C*-values ranging *c.* 2400-fold. Unlike gymnosperms and pteridophytes, the *C*-values of angiosperms are strongly skewed towards small genomes (Fig. 1).

2. Techniques to estimate nuclear genome size in plants

While several methods have been used to assess plant GS, only two have been routinely used. Most of the earlier measurements were done by Feulgen microdensitometry (Greilhuber, 2008). This method quantifies the amount of light absorbed by isolated nuclei that have been fixed on a microscopic slide and quantitatively stained with a DNA-specific dye (usually the Schiff's reagent). The major advantages of Feulgen microdensitometry are as follows: the ability to visually check nuclei before measurement so that their quality can be checked; its applicability to single cells; and the option to store analysed material. However, it has two major drawbacks: (1) it is time-consuming, which precludes its application to large population studies, and (2) it is sensitive so that

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Table 1 Glossary

Alien species (exotic, nonindigenous, nonnative) are those species that have been introduced to a region outside their native distribution range by human activities; they are not necessarily invasive (Richardson *et al.*, 2000; Blackburn *et al.*, 2011).

Biosecurity is the management of risks posed by organisms to the economy, environment and human health through exclusion (the prevention of initial introduction of a species), mitigation, adaptation, control and eradication.

Genome size is a collective term for either holoploid or monoploid genome size. It can also be referred to as nuclear DNA amount or nuclear DNA content. Genome size can be expressed either as the total number of nucleotide base pairs, typically in megabases (Mbp), or in picograms of DNA (1 pg = 978 Mbp).

Holoploid genome size is the amount of DNA in the whole chromosome complement of the nucleus with a chromosome number *n*, irrespective of the degree of generative ploidy. It is abbreviated as the *C*-value. For quantitative comparisons, a prefix number indicating the amount of DNA replication should always be used. For instance, the 1*C*-value and 2*C*-value refer to the amount of DNA in an unreplicated gametic and somatic nucleus, respectively.

Invasive species are a subset of alien species that have become naturalized in a region to which they were introduced, sustaining self-replacing populations, producing reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and having the potential to spread over long distances (Richardson *et al.*, 2000; Blackburn *et al.*, 2011).

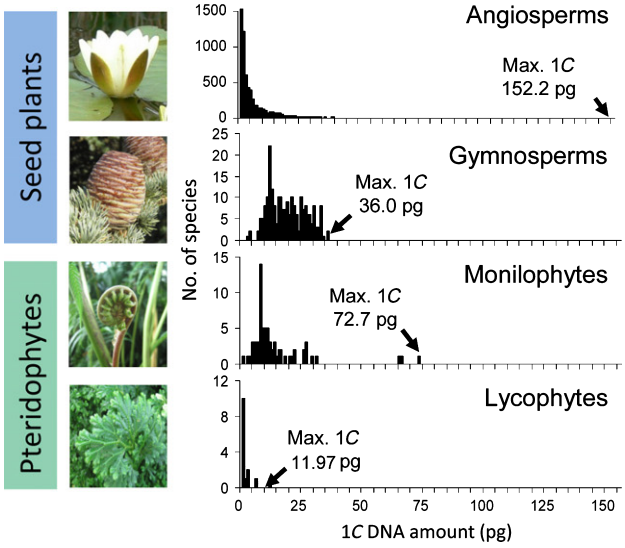
Minimum generation time is the minimum duration of the period from germination until the production of the first seed.

Monoploid genome size is the amount of DNA in one chromosome set of an organism. It is abbreviated as *Cx*-value. In diploid organisms, the 1*Cx*-value is the same as the 1*C*-value, whereas in polyploids, the 1*Cx*-value is always smaller than the 1*C*-value, and is derived by dividing the 2*C*-value by the degree of ploidy.

Naturalized species are those alien species that sustain self-replacing populations for several life cycles or a given period of time (10 yr is advocated for plants) without direct intervention by people, or despite human intervention (Richardson *et al.*, 2000; Blackburn *et al.*, 2011).

Range expansion is the process whereby a species spreads into new areas (usually new regions, rather than local-scale movements) owing to natural- or human-mediated dispersal; such expansion may be assisted or primarily driven by human-mediated changes to the environment. It differs from invasion in that human-mediated extra-range dispersal (i.e. across a biogeographical barrier) is not implicated; the concept can be applied to both native and alien species.

Risk assessment is the estimation of the quantitative or qualitative value of risk (the likelihood of an event occurring within a specified time frame and the consequences if it occurs). In the context of invasion science, risk assessment is undertaken to evaluate the likelihood of the entry, establishment and spread of a species (intentionally or accidentally) in a given region.



Range (pg)	Mean (pg)	Median (pg)	Chromosome numbers (2*n*)	Polyploidy
c. 2400-fold (0.06–152.23)	5.9	2.5	4–*c.* 640	Very common (2*x*–80*x*)
16-fold (2.25–36.00)	18.1	17.2	14–66	Rare (2*x*–8*x*)
94-fold (0.77–72.68)	12.8	9.2	18–*c.* 1440	Common (2*x*–96*x*)
136-fold (0.09–11.97)	2.4	2.0	14–*c.* 520	Intermediate (2*x*–50*x*)

Fig. 1 The distribution of genome sizes (1*C*-values) for vascular plants with summary information on the mean, median and range of 1*C*-values, frequency of polyploidy and range of chromosome numbers.

erroneous measurements have often been reported when stringent best-practice methods were not followed (Greilhuber, 2005, 2008).

In recent years, DNA flow cytometry (FCM) has become increasingly popular as a tool for GS estimation in plant samples and this trend is likely to continue (Bennett & Leitch, 2011). In general, FCM enables highly reliable estimates of nuclear DNA amounts to be made and is therefore recommended as a method of choice, especially when small differences between individuals need to be reliably demonstrated. FCM measures the intensity of fluorescent light emitted from single particles, usually isolated plant nuclei that have been quantitatively stained by a DNA-specific fluorochrome, during their passage through a powerful beam of light (Galbraith *et al.*, 1983). The popularity of FCM arises from its potential for high data throughput, easy sample preparation, ability to analyse tiny plant samples, and high accuracy. These clearly outweigh potential disadvantages, including an inability to visually check the quality of nuclei that are analysed and the need for fresh material in many applications (although dehydrated tissues, fixed

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samples and/or resting seeds have been used in some types of analysis; Suda & Trávníček, 2006; Kolář *et al.*, 2012). Not surprisingly, available *C*-values for a subset of the most widely distributed globally invasive plant species listed by Weber (2003) have mostly been estimated by FCM, followed by Feulgen microdensitometry (Supporting information, Fig. S1).

II. Genome size research meets invasion science: ecological, phenotypic and evolutionary consequences of variation in the amount of nuclear DNA in plants

1. Theoretical basis for a relationship between GS and invasiveness

The search for determinants of invasiveness has always been central to invasion biology (Rejmánek, 1996, 2000). This has usually been explored by comparing traits of invasive and noninvasive species (reviewed by Pyšek & Richardson, 2007). However, achieving this goal has proved difficult, in part because invasions proceed through three distinct but continuous stages (introduction, naturalization and invasion spread), each of which can be driven by different sets of functional traits (Richardson *et al.*, 2000; Richardson & Pyšek, 2012). Traits that confer an advantage at one stage may be neutral or even detrimental at another (Williamson, 2006). In addition, the effects of individual plant species is moderated by introduction histories, differences in propagule pressure (Kolar & Lodge, 2001; Lambdon *et al.*, 2008; Pyšek *et al.*, 2009b), as well as by microevolutionary processes such as interspecific hybridization, introgression, and polyploidy (te Beest *et al.*, 2012).

Recent advances in understanding the traits promoting invasion success have primarily been achieved through analyses of trait differences between alien/native and invasive/noninvasive plant species. Such studies have countered the initial scepticism of this approach and enabled general patterns to emerge (Pyšek & Richardson, 2007; Pyšek *et al.*, 2009a,b; van Kleunen *et al.*, 2010; Küster *et al.*, 2010). Overall, these studies have found that invasive plants are more likely to be tall, exhibit fast growth rates (including vigorous seedling and spatial growth), and have high fecundity and dispersal ability (e.g. small propagules). Life form and evolutionary history also play a role, as more invaders recruit from annuals and from some graminoids. Other characteristics typical of invasives include long flowering periods, resistance to herbivory, and physiological traits such as high specific leaf area, photosynthetic rate, and nutrient- and water-use efficiency.

As the number and availability of GS estimates have increased, so have attempts to incorporate this cytogenetic character into the framework for predicting invasiveness. These began in the 1990s with the suggestion that small genomes favour invasiveness (Rejmánek, 1996). Since then, a growing body of work continues to support this relationship (e.g. Bennett *et al.*, 1998; Knight & Ackerly, 2002; Kubešová *et al.*, 2010; Kuester *et al.*, 2014; Pandit *et al.*, 2014; see Section II.2).

Genome size is included as an explanatory variable because it can constrain many functional traits related to individual growth, reproductive success, and dispersal (Gregory, 2001; Greilhuber & Leitch, 2013). Owing to its effects on cell size parameters and cell division rates, GS affects both size- and rate-dependent traits, and, importantly, it does so across a diverse array of unrelated traits (Fig. 2; Table 2). Of particular importance to invasion potential are the relationships between GS and minimum generation time (Bennett, 1972; Leitch & Bennett, 2007), seed characteristics (Grotkopp *et al.*, 2004; Beaulieu *et al.*, 2007b), relative growth rate of seedlings (Grotkopp *et al.*, 2004), specific leaf area (Morgan & Westoby, 2005; Beaulieu *et al.*, 2007a), and stomatal size and density (which affect water-use and photosynthetic efficiency; Beaulieu *et al.*, 2008; Hodgson *et al.*, 2010). The general trend emerging from these analyses is that species with small genomes can attain a much wider array of trait states compared with species with large genomes, because trait options become more limited as GS increases (the 'large genome constraint' hypothesis; Knight *et al.*, 2005). For example, large-genome plants are obligate perennials whereas their counterparts with small genomes can adopt any life cycle strategy (Bennett, 1972). Similarly, in a broad-scale comparative study, Beaulieu *et al.* (2007b) noted that while a wide range of seed sizes was found in species with small genomes, very small (and thus easily dispersed) seeds were never associated with very large genomes, possibly indicating a developmental constraint. Stomata size, the rate of stomata opening and closure (both scaling positively with GS), and density (scaling negatively with GS) considerably influence carbon fixation and water-use efficiency (Beaulieu *et al.*, 2008), ultimately restricting the range of suitable environmental conditions for a given plant species. In addition, nutrient-poor soils can select against large-genome species because of higher demands for phosphorus and nitrogen to build DNA (Šmarda *et al.*, 2013; Leitch *et al.*, 2014).

Clearly, many traits associated with large genomes do not seem to be compatible with the characteristics of a successful invader. Not surprisingly, Rejmánek (1996, 2000) assumed that a small genome was an important prerequisite for plant invasiveness and

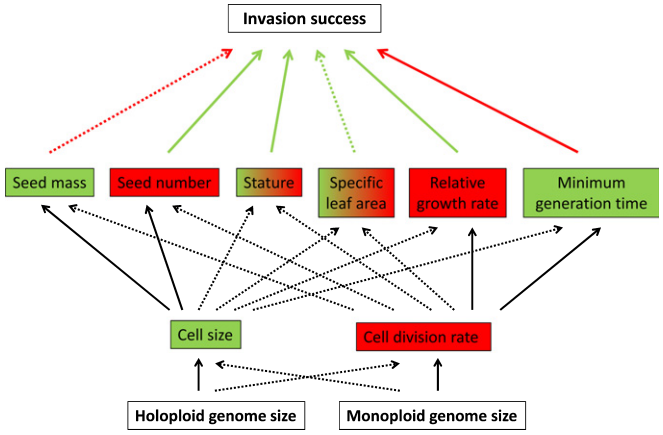

Fig. 2 Multifaceted interactions between holoploid (primarily affecting size parameters) and monoploid (primarily affecting rate parameters) genome size and selected plant traits known to influence invasiveness. Green and red boxes indicate positive and negative relationships of traits with genome size, respectively. Green and red arrows indicate positive and negative relationships of plant traits with invasive potential, respectively. Solid lines denote strong effects, while dotted lines denote weak effects.

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Table 2 Plant traits consistently associated with invasiveness and their relationships with genome size

Plant trait	State favouring invasiveness	Relationship with genome size
Minimum generation time	Short	Positive
Seed mass	Low	Positive
Stature	Tall	None to weakly negative
(Seedling) growth rate	Fast	Negative
Water- and nutrient-use efficiency	High	Negative
Seed number	High	Negative
Specific leaf area	High	Ambiguous (negative in gymnosperms, positive in angiosperms)
Photosynthetic rate	High	Ambiguous (negative in gymnosperms, none in angiosperms)
Flowering period	Long	Unknown
Resistance to herbivory	High	Unknown
Plant defence chemistry	High	Unknown

Small genomes clearly confer a selective advantage. Traits are selected based on Pyšek & Richardson (2007), van Kleunen *et al.* (2010) and other papers mentioned in the text. The relationship with genome size is based on prevailing evidence in the literature (see Section II.1).

listed GS among the eight best predictors of invasion success, arguing that selection for short minimum generation times would be advantageous, particularly for those plant species competing in 'time-limited' environments (Rejmánek *et al.*, 2005). However, as GS can also affect several traits with potentially conflicting roles in plant invasiveness (for instance, it tends to scale positively with seed mass while the opposite is true for seed number; Beaulieu *et al.*, 2007b), its effects on the invasion potential of a plant are likely to be complex (Table 2). Thus, whether a plant becomes naturalized or invasive in a new region will depend on many interacting factors, both biotic and abiotic, of which cytological characteristics (incl. GS variation) are just one facet. Furthermore, global environmental change may yet again alter relationships and interactions as communities and their ecosystems reorganize under new selective pressures.

2. Insights into phenotypic and GS variation in invaders: interspecific comparisons

That variation in interspecific GS potentially plays a role in plant invasiveness is indicated by simply comparing the distribution of genome sizes among invasive and noninvasive plants. A robust insight can be gained because plants that are invasive in global terms (Weber, 2003) are well represented in the Plant DNA *C*-values database (Bennett & Leitch, 2012); of the 450 taxa that are invasive in semi-natural habitats in at least one region of the world, the database and published papers not yet incorporated into the database contain GS data for 242 of these (Table S1). The comparison of frequency distributions of these invasive taxa with data for all angiosperms indicates that noninvasive plants are less strongly skewed towards small genomes (Fig. 3a,b), and small

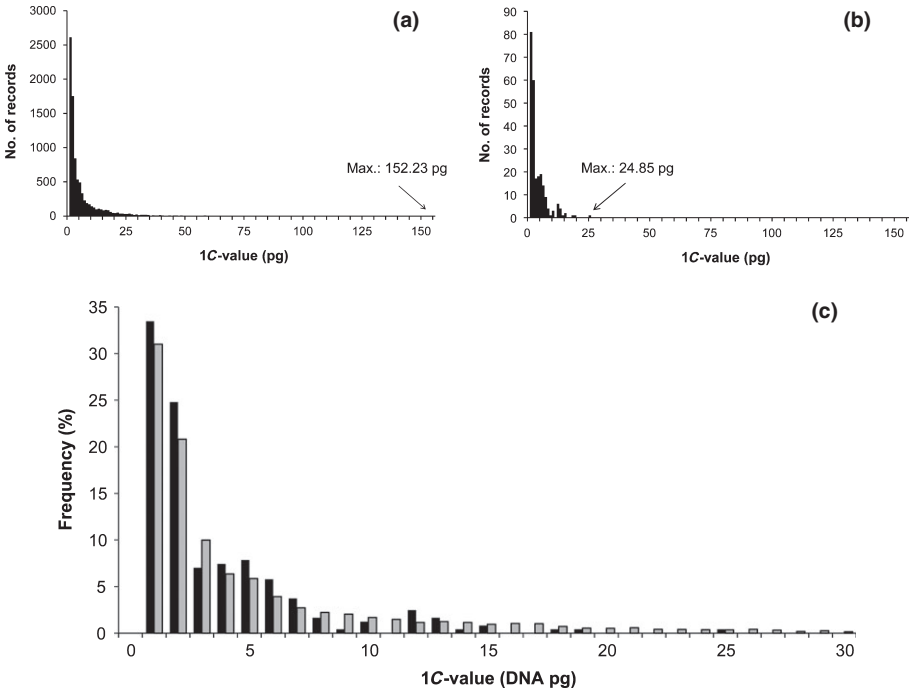

Fig. 3 Distribution of 1*C*-values: (a) in 8658 taxa of angiosperms (based on release 6.0 of the Plant DNA *C*-values database together with data taken from a further 117 publications but not yet incorporated into the database; M. D. Bennett & I. J. Leitch, unpublished); and (b) in 242 taxa out of the 450 listed in Weber (2003) as globally invasive in semi-natural habitats in at least one region of the world. (c) Detailed comparison restricted to taxa with 1*C*-values < 30 pg, as this includes all 242 invasive taxa with genome size data. The plot highlights how very small genomes are relatively over-represented in invasive taxa. Black bars, globally invasive; grey bars, all angiosperms.

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genomes are disproportionately over-represented in the range where invasive taxa fall (Fig. 3c). Both distributions are significantly different (Kolmogorov–Smirnov two-sample test: $D = 0.1196$, KSa = 1.8346, Pr > KSa = 0.0024).

A more rigorous comparison is provided by using a subset of data comprising the 128 most widely distributed invasive species (i.e. species listed in Weber (2003) that occur in more than three regions of the world); GS data are available for 65 of these species (comprising 89 records as a result of intraspecific ploidy/genome size variation; Table 3). If the 1*C*-values of the globally most invasive vascular plants are compared with their noninvasive counterparts (i.e. species not listed in Weber, 2003; Table 3), there is clearly a higher frequency of species with very small genomes ($1C < 1.40$ pg) and a lack of large ($1C > 14$ pg) and very large ($1C > 35$ pg) genomes among invasives (GS categories according to Leitch *et al.*, 1998). The largest known holoploid genome among these most widely distributed globally invasive angiosperms is in the highly polyploid *Tradescantia fluminensis* ($1C = 12.93$ pg), while the largest monoploid genome is in diploid *Nicotiana glauca* ($1Cx = 5.33$ pg). While we recognize that the globally noninvasive plants in our comparison include some species that can be locally invasive, it seems unlikely that such locally invasive plants with large genomes are driving the overall patterns observed. Hence, our conclusion that invasive species are typically characterized by small and very small genomes is robust. This is supported by several recent cross-species comparative studies that have specifically investigated the role of cytogenetic parameters (including GS) in plant invasiveness. For example, in >3500 angiosperms, both *C*- and *Cx*-values had significant effects on plant invasiveness in most studied plant groups, with the exception of trees (possibly because of their long life span) and the family Fabaceae (Chen *et al.*, 2010). Not only did all classes of weed species in this study possess smaller genomes than their nonweedy counterparts, but the sizes of both holoploid and monoploid genomes decreased considerably with increasing invasiveness from common weeds through principal weeds up to serious weeds (based on the categories of Holm *et al.*, 1979). There were no serious herbaceous weeds with large or very large genome sizes. Polyploids were overrepresented among the weeds and the *Cx*-value had a higher predictive power than the *C*-value, at least partly as a result of downsizing of the monoploid GS following polyploidization (Chen *et al.*, 2010).

That invasiveness is negatively correlated with GS but positively with ploidy level (and chromosome number) was also the take-home message of the recent study based on a survey of 890 species defined as invasive based on their inclusion in the Global Invasive Species Database (http://www.issg.org/database) and the Pacific Island Ecosystems at Risk list (http://www.hear.org/pier/scientificnames/scinamea.htm) (Pandit *et al.*, 2014). Although both traits are apparently in conflict with one another (as polyploidy at least initially leads to an increase in 1*C*-value), it is their interaction that underlies their actual effects on plant phenotype and physiology, and ultimately on invasion success. Including both GS and ploidy level in explanatory models turned out to greatly increase their power to predict invasiveness (Pandit *et al.*, 2014).

Research focused at the regional level had results similar to the studies described earlier conducted at the global scale. Kubešová *et al.* (2010) compared 1*C*-values of nearly 100 alien species naturalized in the Czech Republic with their congeners and confamilials not reported to be naturalized or invasive elsewhere. Naturalized species were characterized by smaller *C*-values than their congeners and confamilials that had not successfully naturalized. However, these authors addressed the issue of GS for two stages of invasion and found no significant difference between the values of naturalized (but noninvasive) and invasive species. This suggests that small genomes may be important for promoting successful establishment outside the native range (i.e. naturalization) but less important during the transition from naturalized to invasive species, leading to their massive spread.

Another regional study used chromosome data (i.e. the highest chromosome number standardized by genus, HCNSG) as a surrogate for GS (and, in part, polyploidy), together with time since introduction and seed mass, to predict the likelihood of 7866 cultivated vascular plant species of Hawaii becoming naturalized, weeds or noxious weeds (Schmidt & Drake, 2011; based on data for Hawaii from the Plants National Database (http://plants.usda.gov) and the Hawaiian Ecosystems at Risk Project (http://www.hear/org)). The authors found differences in the predictive values of the three traits for noxious weeds compared with weeds and naturalized species. For example, HCNSG was shown to be the best single predictor for noxious weeds but the worst for predicting naturalized species and weeds. By contrast, the minimum time since introduction was shown to be more successful in predicting the ability of a plant to become naturalized. Overall, a combination of small seed size and high value for HCNSG (which most likely reflects the prevalence of polyploidy) was shown to be the best predictor for noxious weeds. This observation supports the previously reported relationship between polyploidy and invasiveness (te Beest *et al.*,

Table 3 A summary of 1*C*-values (in pg) of the most widely distributed globally invasive species (occurring in more than three regions of the world; Weber, 2003) and globally noninvasive vascular plants (i.e. those not listed in Weber, 2003)

	Globally noninvasive				Globally invasive			
	Range	Mean	Median	Number of records	Range	Mean	Median	Number of records
Pteridophytes	0.09–72.68	10.63	7.95	128	–	–	–	–
Gymnosperms	2.25–36.00	17.90	16.40	345	21.92–28.90	24.30	23.71	10
Angiosperms	0.06–152.23	5.83	2.23	7463	0.25–12.93	2.39	1.48	79

Note that the number of species is lower than the number of available records mainly because of reported intraspecific ploidy/genome size variation.

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2012). Nevertheless, the precise role of GS in predicting invasiveness in the Hawaiian flora still remains to be determined, as GS data are largely unknown for cultivated Hawaiian plants.

The largest regional study to date addressed the fundamental question of 'how weeds emerge' by analysing a range of species traits, including GS as one explanatory variable, for 19 180 species within the USA (both weed/invasive and nonweed species) (Kuester *et al.*, 2014). Plants with small genomes were found to be overrepresented among weeds and introduced species, relative to nonweeds and native species. They also identified 15 genera that had significantly higher proportions of weedy species than expected by chance. While these weedy genera represented a wide range of ecological and phenotypic diversity, they all had a predominance of small genomes. In support of this, our search of the Plant DNA *C*-values database (Bennett & Leitch, 2012) revealed that mean 1*C*-values for these 15 genera ranged from 0.59 to 3.60 pg, with nearly 80% of them belonging to the smallest category (1*C* ≤ 1.40 pg; Leitch *et al.*, 1998). This is distinctly smaller than the mean *C*-value for all angiosperms in the database which is 5.83 pg per 1*C* (Bennett & Leitch, 2012).

However, very small genomes were also overrepresented among genera that had fewer weedy species in the USA than expected by chance (Kuester *et al.*, 2014), suggesting that small genomes can be considered a prerequisite for invasive spread, but not necessarily the trigger. Indeed, the only consistent pattern between all these studies comparing invasive/noninvasive plants is that species with large genomes tend to be excluded from being invasive. This observation is supported by studies showing that the probability of a species being an invader declines considerably with increasing nuclear DNA amount. Furthermore, the taxonomic groups containing species with the largest genomes (e.g. Liliaceae, Melanthiaceae and Santalaceae) are notable for their absence from lists of the most troublesome weeds/invasives (Bennett *et al.*, 1998; Chen *et al.*, 2010; Kuester *et al.*, 2014).

Nevertheless, comparative studies at the generic level across different groups of plants still support the contention that small genomes confer a selective advantage for invasiveness. The gymnosperm genus most thoroughly investigated is *Pinus* (pine) which includes species with different degrees of invasiveness, from noninvasive to highly invasive. Studies by Grotkopp *et al.* (2002, 2004) have shown that invasiveness of pines, especially wind-pollinated species, is negatively associated with GS through this trait's relationships with several life-history traits, including seed mass, specific leaf area and (to some extent) relative growth rate. Similar findings were reported in angiosperm genera such as *Artemisia*, based on an analysis of 51 populations of 20 species (Garcia *et al.*, 2008), where an association between small genomes and an increased tendency to invasive spread were documented. The same pattern was suggested for *Briza* (Rejmánek, 1996). Importantly, this relationship does not seem to be limited to seed plants as recent investigations have shown that it also holds for nonvascular plants despite limited data availability. Varela-Álvarez *et al.* (2012) measured DNA amounts in numerous individuals and populations of three species of *Caulerpa*, an invasive marine green-algal genus in the Mediterranean Sea, and concluded that a reduced GS had contributed to their successful invasion.

However, the link between GS and invasiveness may not always be present, particularly in groups with (very) small genomes where the amount of DNA is unlikely to impose any functional constraints. This is perhaps the case for Australian representatives of the genus *Acacia*, where genomes vary from 0.60 to 1.07 pg per 1*C* (Gallagher *et al.*, 2011). No significant differences in the size of holoploid genomes were observed among 71 noninvasive and 21 invasive species, suggesting that, for *Acacia*, GS did not underpin the variation in traits associated with the invasive/noninvasive dichotomy. Instead, the size of the native distribution range and plant height were the most important determinants of invasion success in acacias. Nevertheless, studies of variation in interspecific GS in plant invasions are leading to more detailed and novel insights by coupling GS studies with plant trait studies under different environmental conditions both in nature and in controlled experiments.

3. Insights into phenotypic and genome size variation in invaders: intraspecific comparisons

Assessing the variation in nuclear DNA amounts between invasive and noninvasive genotypes of a single homoploid species can yield important insights into the role of GS in determining invasion success. Such approaches eliminate the confounding effects of genome copy number (when different cytotypes of the same species are compared; te Beest *et al.*, 2012) and/or of distinct evolutionary histories of studied taxa in congeneric/confamilial comparisons. However, this opportunity has only rarely been exploited, largely as a result of the methodological challenges associated with the reliable detection of small differences in GS at the intraspecific level. While > 200 scientific papers have been published reporting intraspecific variation in GS (Šmarda & Bureš, 2010), most of this variation has subsequently been shown to be the result of artefacts caused by poor technique (Greilhuber, 2005), with the main sources of error arising from cytosolic inhibitors interfering with the quantitative staining of DNA, a suboptimal protocol of slide preparation for Feulgen densitometry, and improper standardization or taxonomic heterogeneity. Nonetheless, despite being much less common than once assumed, the last decade has seen an increasing number of studies that have reliably demonstrated intraspecific variation in GS using high-resolution FCM (Greilhuber & Leitch, 2013). However, understanding the ecological significance of GS variation below the species level is still in its infancy, being hindered by the questionable accuracy of older investigations (e.g. Mowforth & Grime, 1989) and by the fact that recent (and more reliable) studies rarely extend beyond recording the existence and spatial distribution of individuals with different *C*-values.

Phenotypic variation in fitness-related traits associated with intraspecific differences in GS have been reported in the literature, but those focused on invasive species are scarce and not always informative. For example, Sugiyama *et al.* (2002) reported variation in seed size, leaf size and 1*C*-values (amounting to 4.1%) among 15 populations of cultivated *Lolium perenne*. While they observed associations between GS and phenotypic traits, the lack of data on GS variation in natural populations in both its native (Europe, western Asia, northern Africa) and introduced (Australia,

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southern Africa, Americas) ranges prevented the authors from drawing firm conclusions regarding the role of GS in influencing the invasiveness of this species.

In looking for direct effects of GS on invasion potential, the study of Lavergne *et al.* (2010) on reed canarygrass (*Phalaris arundinacea*) is particularly noteworthy, as it provides evidence that GS reduction can trigger rapid phenotypic evolution in invasive genotypes of this species. The authors showed that the invasive genotypes of reed canarygrass in North America originated from intraspecific hybridization between introduced European strains. The genomes of six introduced populations were significantly smaller than those of six native populations, although the differences in mean DNA values were quite small (maximum 2.2%) and both genome groups overlapped markedly. The authors also measured several phenotypic traits under controlled experimental conditions and observed a negative relationship between GS and rate of stem elongation. The introduced small-genome plants showed a higher early growth rate, which may confer a selective advantage and increase invasion potential by allowing for the faster rate of canopy expansion. Although further work is needed to assess the generality of GS variation leading to phenotypic change, the study of Lavergne *et al.* (2010) emphasizes the value of incorporating GS data into studies aiming to improve our understanding of the mechanisms driving plant invasions. In summary, the limited data currently available do support the suggestion that changes in GS within a species can lead to genetic novelties and possibly to the establishment of pheno-/genotypes with enhanced invasive ability, but more studies are clearly needed.

4. Identifying an ideal model system for addressing the role of genome size in invasion success

A prerequisite for rigorous investigations into the effects of GS on invasion potential at the species level is the selection of a suitable plant system, and this approach has been recently advocated for invasion biology in general (Kueffer *et al.*, 2013). An ideal candidate species for such a GS study should meet several criteria, including: a widespread distribution in both native and introduced areas (to examine multiple populations across large spatial scales); a large variation in functional traits (to relate variation in GS to phenotypic variation); well-understood evolutionary processes and introduction/invasion history (to span the full range of stages, from naturalization to invasion); easy cultivation under a range of conditions (to allow extensive experimental work); considerable variation in GS at the monoploid level (to delineate distinct groups with sufficiently different nuclear DNA values); and suitability for FCM (to allow accurate GS estimates). In addition, the occurrence of several different cytotypes would be advantageous, as this provides the opportunity to examine interactions between variation in GS and genome copy number, and also increases the range of *C*-values under study.

One genus that promises to satisfy these requirements is *Phragmites*. It is represented among the globally most invasive plants (Weber, 2003) and includes populations with different introduction histories, diverse geographic origins, considerable karyological and GS heterogeneity, and a complex evolutionary history (Saltonstall, 2002; Lambertini *et al.*, 2006, 2012; L. Meyerson *et al.*, unpublished). Extending from the tropics to cold temperate regions in both hemispheres, *Phragmites* is among the world's most cosmopolitan and globally important wild plants. For example, *P. australis* (ssp. *australis* in Eurasia and Africa, and ssp. *americanus* in North America) is an important component of wetland wildlife habitat and provider of ecosystem services where it is native. In its introduced range, which for ssp. *australis* includes North America, Australia and potentially South America (Lambertini *et al.*, 2012), it is frequently considered a noxious invader. Throughout North America, *Phragmites* has spread rapidly over the last two centuries and has converted botanically diverse wetlands into low-diversity common reed stands (Meyerson *et al.*, 2000). Like many invasive species with small GS, invasive *P. australis* colonizes a wide range of environmental conditions, reproduces both sexually and vegetatively by stolons and rhizomes (Meyerson *et al.*, 2000, 2010), and shows a high within-species genetic diversity (Saltonstall, 2002, 2011; Lambertini *et al.*, 2006, 2012; Meyerson & Cronin, 2013). Because both sexual and clonal reproductive strategies contribute to its invasive success, the application of FCM to study this genus offers an exciting opportunity to assess the relative contribution of GS to different reproduction strategies and invasion success – an unexplored research area. Furthermore, the genus *Phragmites* also encompasses several ploidy levels (Goldblatt & Johnson, 1979 onwards) and our recent flow cytometric measurements (J. Suda *et al.*, unpublished) have revealed considerable variation in GS (up to 22%) within tetra-, hexa- and octoploids (based on $x = 12$) within *P. australis* alone. The variation in *Phragmites Cx*-values is much larger than that found in other genera with invasive representatives, promising a deeper insight into the association between the quantity of nuclear DNA and functional traits. Interestingly, sorting of DNA *Cx*-values according to the invasion status of our studied populations suggests that GS may play a role in invasion success of common reed at the intraspecific level.

III. Applications of genome size data in species-level invasion research

Owing to its increased reliability, high throughput and low cost, FCM has the potential to revolutionize the field of invasion biology and, by extension, conservation biology. The taxonomy of invasive species (Pyšek *et al.*, 2013) and the assessment of interspecific hybridization are two research areas that can greatly benefit from the use of GS data.

1. Species identification

The accurate identification of an organism under study is pivotal to all invasion research. Misidentifications could easily bias the results and impede progress in understanding patterns and dynamics of plant invasions (see Pyšek *et al.*, 2013 for examples). While chromosomal data are widely used for decision-making in plant taxonomy (Stace, 2000), the taxonomic and evolutionary significance of variation in GS has only recently been acknowledged (Kron *et al.*, 2007; Loureiro *et al.*, 2010). The advantage of

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GS over karyological data lies in both the much higher data throughput that is possible and a larger variation in most plant groups than chromosome numbers alone, thus resulting in a higher resolution power. For example, while the number of chromosomes varies only *c.* 160-fold in angiosperms, variation in holoploid GS is *c.* 2400-fold (Fig. 1). In addition, at least twofold variation in monoploid GS was recorded for more than one-third of the genera for which there was sufficient coverage of homoploid species (Loureiro *et al.*, 2010). As a result, GS is a useful character for species circumscription and can help to resolve complex taxonomic problems at and below the species level. Moreover, variation in GS can be viewed as an indicator of taxonomic heterogeneity, incipient speciation or complex evolutionary history. Many taxonomically challenging genera (e.g. *Centaurea*, *Pilosella*, *Taraxacum*; Weber, 2003; Pyšek *et al.*, 2013) include both invasive and noninvasive species that are difficult to distinguish using conventional morphological approaches but show considerable differences in the size of their nuclear genomes. Consequently, GS can be used as a species-specific marker and help to guide taxonomic judgements.

2. Hybrid identification

Interspecific hybridization may serve as a stimulus for the evolution of invasiveness and there are a remarkable number of cases in which hybridization has preceded the emergence of successful invasive populations (Ellstrand & Schierenbeck, 2000; Vilà *et al.*, 2000). Provided that parental species differ sufficiently (6–8%) in GS, the hybrid status of species/populations can be easily determined by estimating nuclear DNA *C*-values. For example, Jeschke *et al.* (2003) reported the existence of homoploid crosses in weedy *Amaranthus* where previous attempts to confirm hybridization using other techniques were unsuccessful. Similarly, while conventional karyological studies did not yield a sufficient degree of resolution, GS data provided evidence for interspecific hybridization between two introduced *Hieracium* subgenus *Pilosella* species in New Zealand (Morgan-Richards *et al.*, 2004) and between the phenotypically similar and globally invasive grass species *Elytrigia repens* and *E. intermedia* (Mahelka *et al.*, 2005). Increased competitive and regenerative ability and faster spread of the hybrid relative to its parents were also documented in *Fallopia* subgenus *Reynoutria*. While misidentifications in this group were common using morphological characteristics (Pyšek *et al.*, 2001), GS offered a much more reliable alternative (Suda *et al.*, 2010).

Genome size data could be particularly helpful in expediting the identification of hybrids for species such as *P. australis*. When this plant was first identified as introduced in North America (Chambers *et al.*, 1999), it was thought that the introduced and native strains could not interbreed because the genetic approaches used failed to detect hybridization; the absence of hybridization was assigned to a phenological barrier. However, a decade later, the analysis of microsatellite data on controlled crosses has shown that interbreeding is indeed possible (Meyerson *et al.*, 2010, 2012) and that both intraspecific hybridization for *P. australis* and interspecific hybridization within the genus *Phragmites* have occurred in the Gulf Coast (Lambertini *et al.*, 2012) and at least at one location in the northeast (Saltonstall *et al.*, 2014). Hybridization in this species is a concern not only because of potential heterosis, but also because native populations are declining and considered to be threatened by pollen swamping and hybridization (Meyerson *et al.*, 2010, 2012). The documented variability in GS described earlier for this species makes it an ideal system where the use of FCM can greatly facilitate the identification of hybrid populations in the future.

3. A new tool for biological security

Biosecurity, the management of risk arising from the introduction or spread of organisms or their genomic material (see Table 1), has received much attention in the invasion literature (see reviews by Meyerson & Reaser, 2002, 2003; Hulme, 2011) – often with the conclusion that comprehensive biosecurity approaches are prohibitive because of costs. However, one approach that could overcome this problem is flow cytometry, as it can provide rapid and low-cost estimates of GS values that can potentially be used to identify invasive plants before introduction. For example, the finding that genome sizes of invaders are restricted to the bottom 20% of the range known for angiosperms (Bennett *et al.*, 1998; Bennett & Leitch, 2005) is information that can be valuable for 'quick and dirty' predictions of invasiveness. In addition, GS can be used as a marker to identify new alien species that cannot be easily distinguished from their native congeners using morphology. Screening for variation in GS can be done in large population samples and across large spatial scales, making FCM a useful exploratory tool in invasion studies. Unlike molecular techniques, protocols for GS determination are simple and usually do not require special laboratory skills, opening possibilities for routine screening of *C*-values in biomonitoring practice. Because differences in GS between putative parents can affect the reproductive biology of hybrids, knowledge of nuclear DNA amounts can also be used to predict the risk of interspecific hybridization. For example, a marked decline in the seed set of hybrids in the genus *Anigozanthos* occurred with increasing GS differences between the parents, with no fertile hybrids produced above a cutoff of *c.* 30% (Le Roux *et al.*, 2010). The authors concluded that parental species with similar-sized genomes should not be grown together in order to prevent interspecific hybridization and the establishment of crosses with increased invasion potential.

IV. Effect of climate change on genome size and invasion success

Available evidence for the association between GS and plant traits, such as maximum photosynthetic rate, specific leaf area, relative growth rate, tolerance to temperature range and frost, and minimum generation time, allows the formulations of hypotheses regarding the role GS will play under ongoing global environmental change and future invasions. Grime & Mowforth (1982) noted phenological differences in the rate of leaf expansion among herbaceous species; those with large genomes tended to grow in early spring, but as the growing season progressed, actively growing

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species had increasingly smaller *C*-values (Grime & Mowforth, 1982; Bennett & Leitch, 2005). As the large genome constraint hypothesis predicts (Knight *et al.*, 2005), evidence also indicates that plant species with small genomes are geographically more widely distributed and inhabit more diverse habitats than those with large genomes. Furthermore, lineages with the largest genomes diversify more slowly and have a higher risk of extinction than those with smaller genomes (Vinogradov, 2003). While data do not support the conclusion that GS is the underlying mechanism for plant success and adaptability, they do beg the question of whether climate change will selectively favour plants with small genomes over those with large genomes. And by extension, as small GS is a trait of invasive plants, will global climate change promote new invasions or range expansions?

Although GS is only one facet of plant success, species with large genomes have reduced maximum photosynthetic rates relative to those with small genomes, and are also excluded from extreme (very cold, hot or dry) environments (Knight & Ackerly, 2002), which are likely to increase in some regions under climate change. The fact that environmental conditions (i.e. precipitation and temperature) have a disproportionate effect on plant species with large genomes suggests that tolerance to climate change will also disproportionately determine 'when, where, and how plants grow' (Leitch & Bennett, 2007), possibly decreasing niche space for species with larger genomes (Fig. 4).

Limited published data suggest that, under climate change, some genomic variants within a species may more successfully cope with changing external filters (e.g. temperature, salinity, drought), owing to greater phenotypic plasticity. As such, some GS variants may be favoured by natural selection, leading to changes in the GS structure of a species over its range, particularly at its range limits. While intraspecific ploidy diversity is common for many angiosperms (Suda & Herben, 2013) and different cytotypes may function as separate ecological entities with variable effects on interspecific interactions (Thompson *et al.*, 1997; Thompson & Merg, 2008; Těšitelová *et al.*, 2013) and different responses to global change, little is known about fine-scale differences in GS at the intraspecific level and how climate change may favour one over the other. At a global scale, few studies provide insights into how climate change may influence the fitness, invasibility and potential for range expansion of related homoploid species that possess different amounts of nuclear DNA (but see Antonelli *et al.*, 2010). Overall, the changing patch- and global-scale geographic mosaics of GS diversity resulting from species introductions and global change are not well documented, yet are critical to understanding how novel webs of interacting species will organize in the future (Thompson, 2009). While climatic-niche requirements of invasive plant species generally seem to be conserved between their native and invaded ranges (Petitpierre *et al.*, 2012), nothing is known about whether the degree of conservatism is similar for plants with different genome sizes.

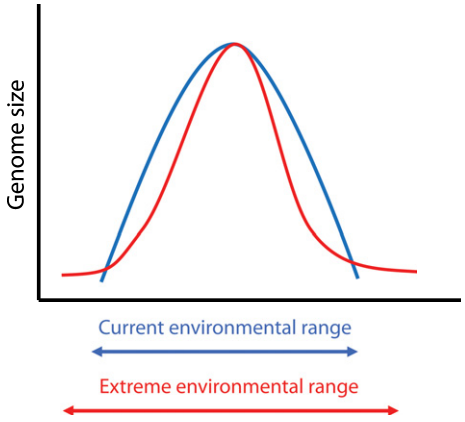

Fig. 4 The large genome constraint hypothesis predicts that populations with large genomes are restricted to narrower environmental ranges because they do not thrive in extreme environments. On the other hand, smaller genomes do not face the same constraints and are more widely distributed. The blue curve indicates the distribution of plants with different genome sizes along the environmental gradient (based on Knight & Ackerly, 2002). Because global climate change is likely to increase areas of environmental extremes, niche space for species with large genomes will possibly decrease (red curve).

V. Gaps in knowledge and avenues for future research: towards closer integration of genome size knowledge into invasion ecology

While much progress has been made in FCM technology and GS research, greater insights are almost certainly possible through the integration of GS studies into taxonomic research, manipulative experiments in global change biology, and invasion ecology. Below we briefly describe several important areas that warrant further research.

1. Intraspecific variation in GS over large spatial scales

The assessment of population-level GS variation in suitable model invasive plants across large spatial scales, including latitudinal and altitudinal gradients, can provide insights into mechanisms conferring invasiveness at the intraspecific level. Because invasions occur at the population (not species) level, studies are needed to determine whether and how invasive potential at the population level relates to GS. To date, this has only been studied for six populations of *P. arundinacea* (Lavergne *et al.*, 2010). Given that intraspecific variation in GS is reported to sort along altitudinal gradients for some, not necessarily invasive, species (e.g. Díez *et al.*, 2013), better performance of certain GS variants in some environments cannot be excluded, despite the failure of the first studies on this topic to demonstrate ecological adaptivity of GS (e.g. Šmarda *et al.*, 2007). In addition, if an association between genome downsizing and invasion potential is found, these geographic data could be used to identify populations with increased invasion potential, particularly those at range edges, and could inform predictions of invasiveness and improve management prioritization. The capacity for such studies would be greatly enhanced by the development of affordable portable flow cytometers that allow direct *in situ* analyses to select diverse, unusual and interesting samples than can be analysed later using

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more time-consuming and expensive techniques (e.g. molecular or analytic).

2. Incorporating GS data in macroecological studies of species invasiveness

Comparative macroecological analyses aimed at identifying factors that determine species invasiveness are a common tool in invasion biology and have contributed to the theory (see Pyšek & Richardson, 2007 for review). These studies are, however, limited by available data that are often lacking for important traits (such as those related to reproduction; see Moravcová *et al.*, 2010), and the results are affected by which traits are used as predictors of invasiveness (Pyšek & Richardson, 2007). Given that GS is only one factor promoting invasiveness, its real importance can only be identified if it is tested in concert with other traits, as well as factors known to affect invasion outcomes, such as propagule pressure and residence time, and their complex interactions (Pyšek *et al.*, 2009a, b). Therefore, large-scale and reliable datasets on GS variation (ideally for entire floras) are needed to routinely include GS as a factor in macroecological analyses. Nevertheless, it is noted that such approaches may be complicated because the available published data can be unreliable as a result of different techniques and suboptimal protocols; some data may therefore require reanalysis using best-practice methods (preferably FCM). Large-scale GS invasion studies should include and discriminate among the different stages of invasion (Richardson *et al.*, 2000; Blackburn *et al.*, 2011), as the role of particular traits may differ among the naturalization and invasion stages (Williamson, 2006; Pyšek *et al.*, 2009a,b; Richardson & Pyšek, 2012; Moodley *et al.*, 2013), and there is some evidence that this may be true for GS as well (as noted earlier; see Section I.2; Kubešová *et al.*, 2010).

3. Plant defence and natural enemy interactions

The differences in resistance to pathogens or herbivores among different cytotypes are well known to agriculture (Doležel *et al.*, 2007b), but have received less attention from ecological studies. Although herbivores and pathogens are thought to play an important role in range expansions and plant invasion success (e.g. Keane & Crawley, 2002; Fagan *et al.*, 2005; Menendez *et al.*, 2008; Phillips *et al.*, 2010; Cronin *et al.*, 2014), information on enemy impact and plant defences in relation to ploidy level is limited (e.g. Janz & Thompson, 2002; Halverson *et al.*, 2008; Broz *et al.*, 2009; Hahn *et al.*, 2012), and there are no published data that test whether a relationship exists between GS and allocation of resources to structural or chemical defences. Interactions with natural enemies may be significantly affected by both changes in defence capabilities and altered fitness–defence tradeoffs. Moreover, under climate change, we expect that GS variation and natural enemies will continue to be important drivers of range expansions and species invasions. Therefore, research on all three factors and their interactions is critical to understanding current and future species ranges, and to answer the question: will global climate change exert selective pressures that favour some genome sizes over others?

4. Phylogenetic interactions of GS and other species traits

Whether or not there are phylogenetic patterns or differences in the way that GS interacts with traits conferring invasive potential deserves attention. On a broad scale, the very different GS profiles and incidences of polyploidy and chromosome diversity in different land plant groups suggest that the role of GS may differ between these groups; for example, the mean GS of invasive gymnosperms is significantly larger than that of invasive angiosperms (Table 3). Despite the underlying relationships between, for example, GS and cell size, and cell cycle time, do differences in phylogenetic group translate into different mechanisms operating to influence the role of GS in invasiveness? If so, then perhaps an invasive model species for each land plant group is needed to provide distinct information for each group. At a lower taxonomic scale, the observation that some angiosperm families are over-represented in terms of the number of invasive species they contain (Daehler, 1998; Pyšek, 1998; Kuester *et al.*, 2014) also suggests that GS may interact with phylogenetic factors influencing the invasive potential of a species.

VI. Conclusions

Owing to its effects on many unrelated life-history traits, the last decade has seen a growing interest in the use of GS data as a predictor in ecological studies, including those aimed at identifying the factors underlying invasion success of land plants. Large-scale comparisons relating GS to invasion potential have led to the emergence of some general patterns, yet the evolutionary significance and role of small vs large genomes in plant invasions clearly needs to be more fully understood. The technology to estimate amounts of nuclear DNA is advancing rapidly and becoming more accessible in terms of price and techniques. As a result, the taxonomic, spatial and temporal scope of cytogenetic investigations on invasive plants is widening and promises new insights into the ecological and evolutionary consequences of variation in nuclear GS. Key challenges for future studies are to reveal how GS operates at different invasion stages, how population-level differences in GS vary spatially and/or whether global change will increase invasiveness of some populations/species through selective pressures acting on traits constrained by the size of the nuclear genome. In addition, we envisage more extensive use of GS data in taxonomic identification and biosecurity efforts, making this cytogenetic marker widely available to practitioners. In combination with data on ecology, distribution, genetics, and reproductive biology, increasing knowledge of GS will advance our understanding of factors conferring invasiveness and will open new avenues of investigation in evolutionary and population biology of invasive plant species.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Histogram showing the contribution of main methods to estimate genome size in vascular plants based on prime estimates from release 6.0 of the Plant DNA *C*-values database (Bennett & Leitch, 2012).

Table S1 Selected karyological characteristics (if known), including holoploid (1*C*-value) and monoploid (1*Cx*-value) genomes size, for 242 globally invasive plant species (based on Weber, 2003)

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